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Leaf architecture of subtribe Micheliinae (Magnoliaceae) from China and its taxonomic significance

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Abstract Leaf architectural and morphological characters of 28 taxa from *Michelia*, *Paramichelia* and *Tsoongiodendron* (Magnoliaceae *sensu stricto*, subtribe Micheliinae) were examined to gain a better understanding of the intergeneric relationships and the systematic positions of some species within *Michelia*. The taxa examined, all of which have simple leaves with entire margins and camptodromous pinnate venation, varied in their secondary venation, which was brochidodromous or brochidodromous to eucamptodromous, the mixture of simple and composite intersecondary veins, percurrent to reticulate tertiary veins. Dendroid veinlets were recorded for the first time in *Michelia* species. Phenetic analyses of leaf architectural characters and morphological characters suggested that *Paramichelia* and *Tsoongiodendron* are grouped together and merged in the *Michelia*, and these characters provide useful taxonomic information for division of sections in *Michelia*. In addition, systematic positions of some species in *Michelia* are discussed.

Key words Magnoliaceae, *Michelia*, *Paramichelia*, *Tsoongiodendron*, veinlet, taxonomy.

The family Magnoliaceae is one of the most primitive groups of angiosperms (Takhtajan, 1980; Cronquist, 1981; Endress, 1990), comprising deciduous or evergreen trees or shrubs, characterized by annular stipular scars around the nodes, and floral parts spirally arranged on an elongated receptacle. It comprises sixteen genera and over 300 species widely distributed throughout E and SE Asia, SE North America, Central America and South America. Approximately 11 genera and more than 160 species of Magnoliaceae are found in China (Liu, 2004).

It is generally accepted that Magnoliaceae consists of two subfamilies, Magnolioideae and Liriodendroideae (Law, 1984, 1996; Liu, 2000, 2004; Nooteboom, 1985; Chen & Nooteboom, 1993; Gong et al., 2003; Figlar & Nooteboom, 2004; Sun & Zhou, 2004). There has been persistent debate on the classification of Magnolioideae. Law (1984) recognized two tribes, Michelieae with axillary flowers and Magnolieae with terminal flowers, and fourteen genera. The tribe Michelieae consisted of two subtribes, Elmerrilliinae and Micheliinae. The former contained only the genus *Elmerrillia*, which is easily distinguished by its sessile gynoecium and introrsely dehiscent anthers. Micheliinae, in contrast, with a stipitate gynoecium and laterally dehiscent anthers, consisted of *Michelia* L., *Paramichelia* Hu, and *Tsoongiodendron* Chun. Gong et al. (2003) recognized only two genera: *Magnolia* L. and *Michelia* L., and placed *Magnolia* subgenus *Yulania* (Spach) Reichenb. into *Michelia*. Sun & Zhou (2004) recognized two tribes and two genera. Figlar and Nooteboom (2004) lumped all the genera of Magnolioideae into a single genus *Magnolia*.

Michelia is the second largest genus in Magnoliaceae (Law, 1984) and consists of

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approximately 80 species mainly distributed in tropical and subtropical Asia. Approximately 70 species are found in China, mainly in SW to E China. *Paramichelia* has three species, distributed in tropical and subtropical SE Asia, with one species in SW China. *Tsoongiodendron* is monotypic, *Tsoongiodendron odorum* Chun growing in S China and N Vietnam. The systematic positions of *Paramichelia* and *Tsoongiodendron* have always been uncertain. They were treated as independent genera by Hu (1940), Chun (1963), Dandy (1974) and Law (1984, 1996; Liu, 2004) because of their distinctive, large syncarpous fruits, and were placed into the Michelieae because of their stipitate gynoecia. However, Nooteboom (1985) and Chen & Nooteboom (1993) considered their axillary flower to make them congeneric with *Michelia*. Dandy (1974) established the infrageneric classification of *Michelia* and recognized four sections: *Michelia*, *Micheliopsis* (Baill.) Dandy, *Dichlamys* Dandy, *Anisochlamys* Dandy. Chen and Nooteboom (1993) reduced both *Paramichelia* and *Tsoongiodendron* into synonymy of *Michelia* where they were treated as distinct sections. Law (1996) followed Dandy's classification, and established two subgenera: subgenus *Michelia* with stipular scars and subgenus *Metamichelia* Law & Y. F. Wu without stipular scars. However Law's section *Anisochlamys* is totally different from that of Dandy, or that of Chen and Nooteboom. Chen and Nooteboom (1993) recognized one species of Chinese *Michelia* in section *Anisochlamys*, *M. hypolampra* Dandy. In addition to *M. hedyosperma* Law, a synonym of *M. hypolampra*, Law (1996) included many species in section *Anisochlamys* that had been included in section *Michelia* by Chen and Nooteboom (1993).

Leaf venation can be considered as a two-dimensional ramifying structure. After the fundamental findings on venation pattern and their phylogenetic and histogenetic development established (Ettinghausen, 1861; Gluck, 1919; Troll, 1939; Wylie, 1939, 1943, 1946, 1950; Foster, 1952), attention is paid largely to leaf architecture of fossil and living plants owing to its importance for systematic classification (Dilcher, 1974; Hickey & Wolfe, 1975; Li & Hickey, 1988; Sun et al., 1991; Wang et al., 2001; Luo & Zhou, 2002). In Magnoliaceae, Pray (1954) studied the leaf venation of *Liriodendron* L. in detail and described its venation as mixed-craspedodromous venation pattern. Similar work has been done by other researchers. Hickey and Wolfe (1975) described briefly leaf venation of Magnoliales. Yu and Chen (1991) described leaf architecture of nine genera and twenty species in the family. Liao et al. (2000) described leaf venation of thirty-seven species representing fourteen genera of the family. However, no intensive studies on leaf architecture of *Michelia* have been conducted, so its value in resolving taxonomic problems needs to be explored. The purpose of the present study is to survey leaf architectural characters of Michelieae for a better understanding of the close relationships of *Michelia* and its related genera and infrageneric classification and the systematic position of some species within *Michelia*.

1 Material and methods

Leaves of twenty-seven species and one variety of the three genera *Michelia, Paramichelia*, and *Tsoongiodendron* were studied using low magnification and stereoscopic microscopy. Leaves were obtained from herbarium specimens in South China Botanical Garden, the Chinese Academy of Sciences (IBSC). The vouchers are listed in Table 1.

The method making leaf venation followed that of Yu and Chen (1986). Leaves were boiled in water for 10–20 min, and then placed in 10%–20% NaOH at 80–90 ℃ for 20–30 min. Because leaf texture differs slightly between species, thicker leaves were prepared with higher NaOH concentration. The epidermis and mesophyll were removed with a painting brush, rinsed in water, and bleached in 10% H_2O_2 for 6–8 h. Cleared and bleached leaves

Table 1 Vouchers of specimens examined

Taxon	Locality	Voucher
Michelia alba DC.	Xiamen (厦门), Fujian (福建)	G. D. Ye (叶国栋) 532
M. balansae Dandy	South China Botanical Garden	H. G. Ye (叶华谷) 726
M. cavaleriei Finet & Gagnep.	Yuanyang (元阳), Yunnan (云南)	S. C. He (何树春) 85170
M. champaca L.	Guangzhou (广州), Guangdong (广东)	H. Q. Zhou (周汉泉) 11189
M. chapensis Dandy	Nanxiong (南雄), Guangdong (广东)	Nanzhidi Exped. (南植地队) 48
M. crassipes Law	Guangzhou (广州), Guangdong (广东)	R. Z. Zhou (周仁章) 0006
M. doltsopa Buch.-Ham. ex DC.	Without precise locality, Yunnan (云南)	T. T. Yu (俞德浚) 18055
	Without precise locality, Yunnan (云南)	T. T. Yu (俞德浚) 18055
M. elegans Law & Y. F. Wu	Guangzhou (广州), Guangdong (广东)	Y. Q. Chen (陈有卿) 110
	Guangzhou (广州), Guangdong (广东)	Y. Q. Chen (陈有卿) 115
M. figo (Lour.) Spreng.	Guangzhou (广州), Guangdong (广东)	B. H. Chen (陈炳辉) 312
	Guangzhou (广州), Guangdong (广东)	H. G. Ye (叶华谷) 653
M. floribunda Finet & Gagnep.	Jingdong (景东), Yunnan (云南)	M. K. Li (李鸣冈) 1729
M. foveolata Merr. ex Dandy	South China Botanical Garden	Y. Q. Chen (陈有卿) 59
M. foveolata var. *cinerascens* Law & Y. F. Wu	Without precise locality, Fujian (福建)	C. D. Liu (刘初钿) 83-102
	Without precise locality, Zhejiang (浙江)	M. X. Wu (吴鸣翔) 7720
M. hypolampra Dandy	Without precise locality, Guangxi (广西)	L. Z. Jia & X. L. Feng (贾良智, 冯学林) 6054
M. longistamina Law	Ruyuan (乳源), Guangdong (广东)	S. P. Ko (高锡朋) 53762
M. macclurei Dandy	Lianshan (连山), Guangdong (广东)	B. H. Chen (陈炳辉) 255
M. maudiae Dunn	Guangzhou (广州), Guangdong (广东)	S. H. Chun (陈少卿) 69
M. mediocris Dandy	Guangzhou (广州), Guangdong (广东)	Y. Q. Chen (陈有卿) 64
M. microcarpa B. L. Chen & S. C. Yang	Maguan (马关), Yunnan	R. Z. Zhou (周仁章) 9314
M. microtricha Hand.-Mazz.	Simao (思茅), Yunnan (云南)	Sino-Soviet Yunnan Exped. (中苏云南队) 9187
M. platypetala Hand.-Mazz.	Guangzhou (广州), Guangdong (广东)	H. G. Ye (叶华谷) 694
	Guangzhou (广州), Guangdong (广东)	H. G. Ye (叶华谷) 673
M. skinneriana Dunn	Lechang (乐昌), Guangdong (广东)	Y. Tsiang (蒋英) 1332
	Longmen (龙门), Guangdong (广东)	B. H. Chen (陈炳辉) 19
M. sphaerantha C. Y. Wu ex Law & Y. F. Wu	Without precise locality, Yunnan (云南)	M. K. Li (李鸣冈) 0003
M. szechuanica Dandy	Guangzhou (广州), Guangdong (广东)	H. G. Ye (叶华谷) 711
	Guangzhou (广州), Guangdong (广东)	H. G. Ye (叶华谷) 685
M. velutina DC.	Without precise locality, Xizang (西藏)	W. L. Chen (陈伟烈) 14538
M. wilsonii Finet & Gagnep.	Emei (峨眉), Sichuan (四川)	W. P. Fang (方文培) 15969
M. yunnanensis Franch. ex Finet & Gagnep.	Without precise locality, Yunnan (云南)	T. N. Liou (刘慎谔) 23100
Paramichelia baillonii (Pierre) Hu	Without precise locality, Yunnan (云南)	J. S. Xin (辛景三) 382
Tsoongiodendron odorum Chun	Dinghushan (鼎湖山), Guangdong (广东)	K. C. Ting & G. L. Shi (丁广奇, 石国良) 81

were then rinsed in running water thoroughly, dried, stained in 5% methyl green for 30 min and photographed and evaluated by different powers of stereoscopic microscopy for different orders of vein branching.

The terminology follows that of Hickey (1973, 1979) and conforms to the codification of the Leaf Architecture Working Group (Ash et al., 1999).

Forty-six characters of leaf architecture and morphology (Table 2) were used for phenetic analysis in order to better understand the infrageneric classification of *Michelia* and the relationships between *Michelia* and closely related genera. Thirty-three operational taxonomic units (OTUs) consisted of all taxa surveyed, four species in *Magnolia* (*M. coco* (Lour.) DC., *M. albosericea* Chun & C. H. Tsoong, *M. sprengeri* Pamp., and *M. liliiflora* Desr.), and *Liriodendron chinense*. Twenty-nine characters were scored as binary and

Table 2 Leaf architectural characters and related morphological characters used in the phenetic analyses

1	Laminar shape: elliptic (0), including narrowly elliptic, oblanceolate-elliptic, and rhombic-elliptic; obovate or narrowly obovate (1); oblong, narrowly oblong, obovate-oblong, or narrowly oblanceolate-oblong (2); oblong-elliptic or elliptic-ovate (3); special (4).
2	Apex: acute, acuminate, or cuspidate (0); obtusely acuminate (1); caudate-acuminate (2); truncate (3).
3	Base: cuneate or narrowly cuneate (0); broadly cuneate or obtuse (1); rounded or nearly cordate (2).
4	Lobation: unlobed (0); 2–10 lobed (1).
5	Blade class: microphyll (0); notophyll (1); mesophyll (2).
6	Lamina L:W (length:width) ratio: 0<L:W<2 (0); 2≤L:W≤3 (1); L:W>3 (2).
7	Petiole length: ≤0.5 cm (0); >0.5 cm (1).
8	Venation type: camptodromous pinnate (0); mixed-craspedodromous pinnate (1).
9	Number of secondary veins (pairs): <10 pairs (0); ≥10 pairs (1).
10	Variations in angle of divergence: consistent (0); inconsistent (1).
11	The existence of inter-2° veins: common (0); few (1).
12	Inter-2° veins: simple, occasionally composite (0); composite (1); obscure (2).
13	Tertiary pattern: reticulate (0); alternate and opposite percurrent (1); regular polygonal reticulate (2).
14	Quaternary course: reticulate (0); alternate and opposite percurrent (1).
15	Quintenary course: reticulate (0); alternate and opposite percurrent (1).
16	Areolation: imperfect (0); well developed (1).
17	Areola shape: quadrangular (0); irregular (1); polygonal (2).
18	Areola size (As): 1 μm<As≤2 μm (0); 2 μm<As≤1 mm (1); As>1 mm (2).
19	Number of veinlets in each areola: 1 (0); >1 (1).
20	Veinlets: simple (0); 1–2 times branched (the majority one time branched, few twice branched (1); 2–4 times branched (2); dendroid (3).
21	Marginal veins: incomplete (0); looped (1); fimbriate (2).
22	Higher order veins: 5th (0); 6th (1).
23	Leaf texture: chartaceous (0); coriaceous (1).
24	Stomata: anomocytic (0); anomocytic and paracytic (1).
25	Stipular scars on petioles: present (0); absent (1).
26	Length of stipular scars: less than half of petiole length (0); nearly to half of petioles (1); longer than half of petiole length (2); nearly to petiole length (3); no stipular scars (4).
27	Leaf arrangement: evenly arranged at the twigs (0); crowded into false whorls at the ends of the twigs (1).
28	Habit: evergreen (0); deciduous (1).
29	Young leaf orientation in vegetative bud: erect (0); pendant (1).
30	Branching morphology: sylleptic (0); proleptic (1).
31	Laminar indumentum: glabrous (0); only lower surface appressed indumentum (1); both upper and lower surfaces appressed indumentum (2).
32	Phyllotaxis: spiral (0); distichous (1).
33	Gynophore: absent (0); present (1).
34	Flower position: terminal (0); axillary (1).
35	Number of tepals: nine or more (0); six (1) .
36	Outer and inner tepals: subequal (0); outer tepals less than inner ones (1); outer tepals longer than inner ones (2).
37	Outer 3 tepals: membranaceous and narrower (0); not membranaceous and narrower (1).
38	Outer 3 tepals: calyx-like (1); not calyx-like (1).
39	Flowering time: flowers not precocious (0); flowers appearing at the same time or slightly after leaves (1); flowers precocious (2).
40	Anther dehiscence: introrse (0); latrorse (1); extrorse (2).
41	Gynoecium exposure: not covered by the androecium (0); androecium covering the gynoecium (1).
42	Pre-dehiscence fruiting carpel fusion: separate (0); concrescent (1).
43	Number of ovules in each carpel: 2 (0); > 2 (1).
44	Carpel rib upon carpel dehiscence: dehiscent (0); persistent (1).
45	Fruit type: follicle (0); samaroid (1).
46	Fruit dehiscence: apical parts persistent, carpels splitting mostly via the dorsal/ventral suture (0); apical parts mostly breaking / falling away circumscissile, singly or irregular masses, while also more or less parting along the dorsal / ventral suture (1); indehiscent (2).

seventeen as multi-state. The characters were scored as missing when unavailable. The data matrix is listed in Table 3. All characters were unordered and equally weighted. Phenetic analysis was performed with PAUP* 4.0 b10 (Swofford, 2002) using the Unweighted Pair Group Averages Method (UPGMA).

2 Results

2.1 Leaf architectural characters

2.1.1 Leaf *Michelia*, *Paramichelia*, and *Tsoongiodendron* produce simple, symmetrical,

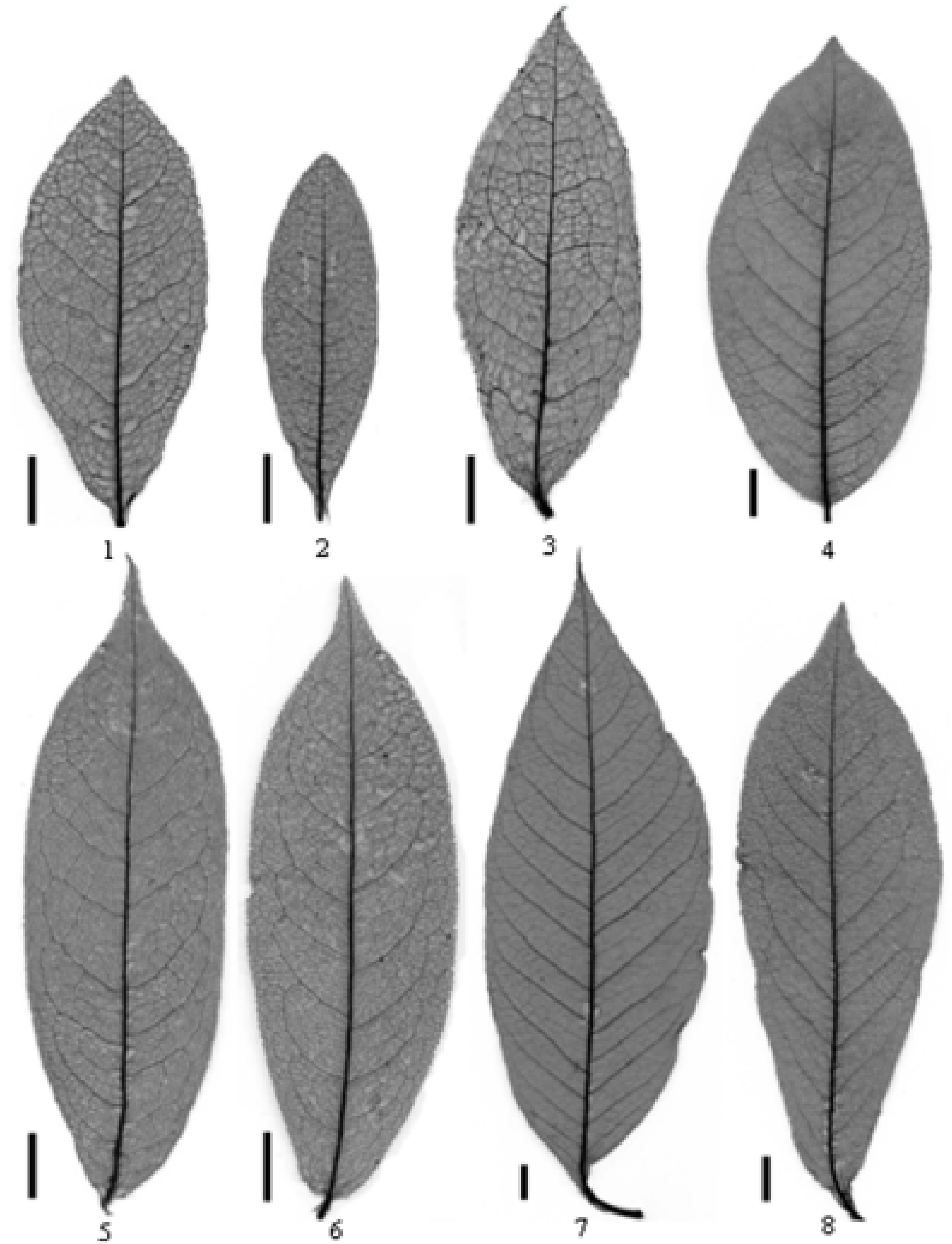
Table 3 Data matrix of characters used in the phenetic analyses*

Taxon	Character states
	11111111112222222222333333333344444444
	12345678901234567890123456789012345678901234567890123456
Magnolia coco	00001210111110000101201002000000000011100010000
Ma. albosericea	0000221011001001010111100200001000021100010000
Ma. sprengeri	1000101001101000010110100011012100001121010000
Ma. liliiflora	1000111001101000010220100101012100011011010000
Michelia alba	0200211010101001210110100100011111001101001000
Mi. balansae	0010211011101000121210101400011111121101001000
Mi. cavaleriei	2000111011102011221300101400012111021101001000
Mi. champaca	0200211011101001210110100200011111001101001000
Mi. chapensis	1000111011101000121200101400010111121101001000
Mi. crassipes	0000010001100000121200100300011111101101101000
Mi. doltsopa	0010111011101001200010100000011111001101001000
Mi. elegans	2010111011101001010100101400011111001101001000
Mi. figo	0000010001120001011110100300011111101101001000
Mi. floribunda	0010111010101001210320100200011111001101001000
Mi. foveolata	3020211011101111010020101400011111021101001000
Mi. foveolata var. *cinerascens*	3020211011101111010000101400011111021101001000
Mi. hypolampra	1000111010101111011310101400010111010101001000
Mi. longistamina	0000111011101001220000101400010111121101001000
Mi. macclurei	1000111010101001210000101400012111021101001000
Mi. maudiae	0110111011101001010000101400010111021101001000
Mi. mediocris	0000111011101001210000101400011111001101001000
Mi. microcarpa	200011101010100101110010140001011111?11???01000
Mi. microtricha	0000111010101001200320100200012111021101001000
Mi. platypetala	2110111011101001020000101400011111021100001000
Mi. skinneriana	0200010001101000121200100300011111101101001000
Mi. sphaerantha	2010201011101001210000101400011111001101001000
Mi. szechuanica	1000111011101001220000101400012111001101001000
Mi. velutina	0110111011101001200000100200012111021101001000
Mi. wilsonii	1000111010101001210100100000011111021100001000
Mi. yunnanensis	1100010001101001011100100300011111121101001000
Paramichelia baillonii	0000111011101001210100100200012111021101011101
Tsoongiodendron odorum	0100211011101011011100100200011111021101111001
Liriodendron chinense	4321101101101001010110111401100000001002010012

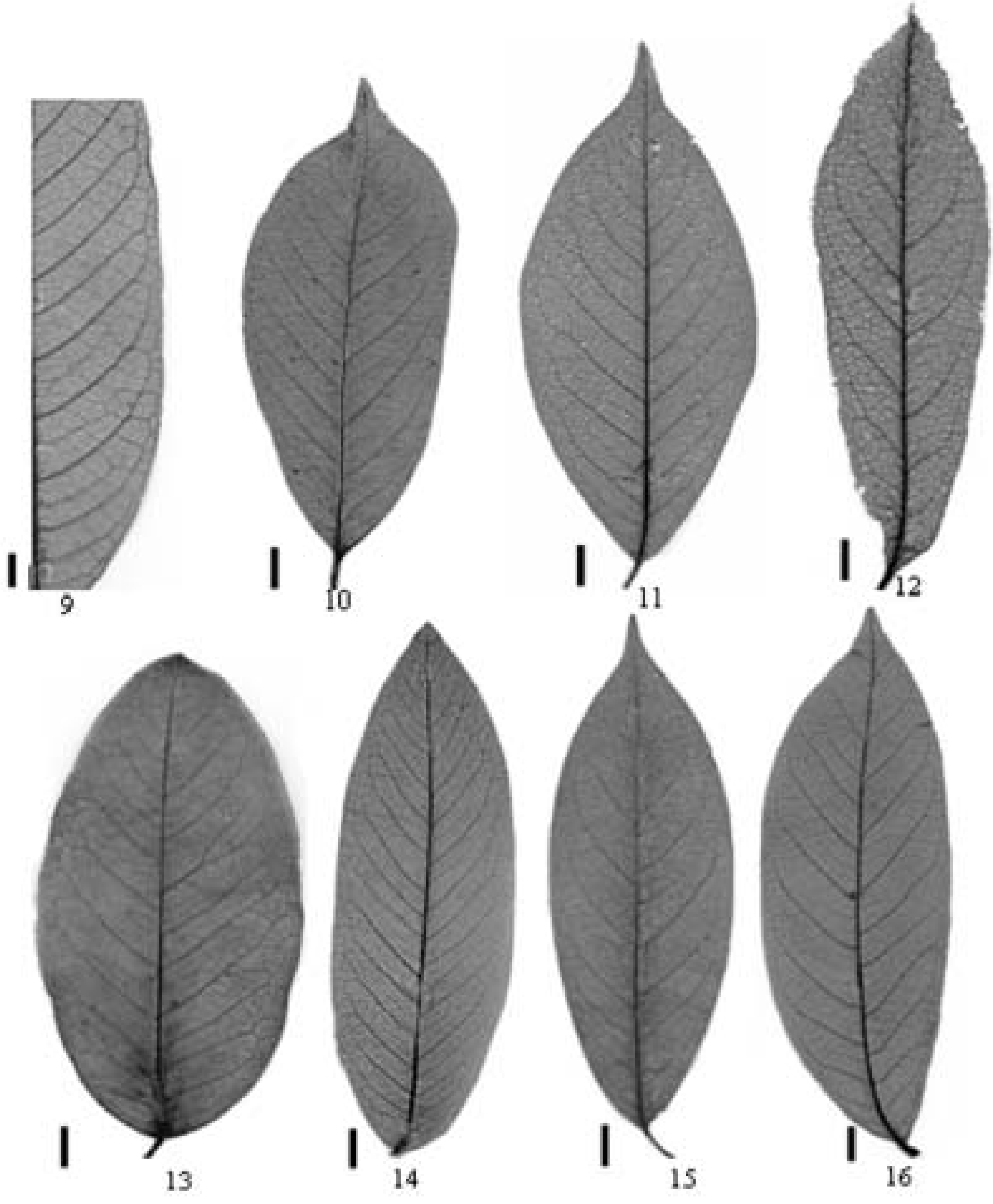
* ? = missing.

entire leaves ranging in size from 4×1.7 cm (length×width) in *M. yunnanensis* to 27×9.5 cm in *M. alba*. Laminar shape is quite variable, being elliptic, narrowly elliptic, narrowly obovate, obovate-elliptic or lanceolate-ovate (Figs. 1–16), with a length to width (l/w) ratio of from 1.8 to 3.2 (mean: 2.49). According to area of leaf in mm^2, three types, microphyll (225–2025), notophyll (2025–4500), and mesophyll (4500–18225) are recognized. The leaf apex is acute, acuminate, obtuse or caudate-acuminate. The leaf base is cuneate, broadly cuneate (Fig. 4), obtuse or rounded (Fig. 13). Leaves are petiolate and petioles are longer than 5 mm with the exception of species in section *Micheliopsis* in which they are less than 5 mm.

2.1.2 Venation pattern The major veins in the taxa examined are camptodromous pinnate. Two basic types of secondary venation pattern can be recognized, brochidodromous and eucamptodromous. Most species possess both brochidodromous and eucamptodromous venation patterns, the latter occurring in two or four pairs of weakly eucamptodromous veins at both ends. Some species only have a brochidodromous venation pattern, e.g., species in section *Micheliopsis* (Figs. 1–3, 5, 6). Occasionally, secondary veins are forked near the margin (Fig. 13).



Figs. 1–8. Cleared leaves of species examined. **1.** *Michelia figo*, arrow showing prominent arch of secondary vein joining to the superadjacent secondary vein. **2.** *M. yunnanensis*. 3**.** *M. crassipes*. **4.** *M. elegans*. P_1, showing alternately reticulate tertiary vein; P_2, showing oppositely percurrent tertiary vein; P_3, showing composite intersecondary vein. **5, 6.** *M. skinneriana*, showing the same leaf architectural characters of the species. **7.** *M. alba*. P_1, showing oppositely percurrent tertiary vein; P_2, showing obscure arch; P_3, showing weakly eucamptodromous vein at the base of lamina. **8.** *M. wilsonii*. Scale bar=1 cm.



Figs. 9–16. Cleared leaves of species examined. **9.** *Michelia balansae*. P_1, showing oppositely percurrent tertiary vein; P_2, showing composite intersecondary vein; P_3, showing 2° divergent angle more obtuse than that at upper part of lamina. **10.** *M. hypolampra*. P_1, showing composite intersecondary vein; P_2, showing simple intersecondary vein. **11.** *M. macclurei*. **12.** *M. platypetala*, showing large areolas in taxa examined in the present study. **13.** *M. foveolata*. The arrow shows secondary vein forked near the end. **14.** *M. velutina*. **15.** *M. floribunda*. **16.** *Tsoongiodendron odorum*, showing primary vein slightly curve at base.
Scale bar=1 cm.

2.1.3 Divergence angle of secondary veins from midveins The divergence angle of secondary veins from midveins of the taxa examined can be grouped into two types, consistent and variable. For the consistent type, the divergence angle of secondary veins from midveins is relatively consistent at about 50˚ (Figs. 7, 8, 10–12, 15). For the variable type, the divergence angle in the distal portion of leaves is more acute than the angle in the proximal portion, progressing from c. 30˚–85˚ from apex to base (Figs. 1–6, 9, 13, 14, 16).

2.1.4 Intersecondary veins and higher order veins Intersecondary veins are usually few and mainly mixed with simple and composite ones (Figs. 4, 9, 10). Tertiary veins are alternate percurrent (Figs. 4, 7), opposite percurrent (Figs. 4, 7, 9), random reticulate (Fig. 3), or regular polygonal reticulate (Fig. 37). Higher order veins are present up to the 5th order, but 4th order veins generally anastomose with 5th order veins to form areolas.

2.1.5 Veinlets The veinlets within the ultimate areolas are usually simple (Figs. 22, 34–36, 38, 39, 41–43), branched 1–3 times (Figs. 27, 28, 29, 33), dendroid (Figs. 19, 20, 37, 40), or occasionally absent altogether (Figs. 24, 39).

2.1.6 Areolas Areolas are well developed or imperfectly closed meshes. They are triangular, quadrangular or irregular in shape. Their sizes vary widely from 1 to 2000 μm. The largest areolas, of 1.5 to 2 mm, were found in *M. platypetala* (Fig. 12). Most species have medium-sized areolas of 2.5 μm to 1 mm (Figs. 17–19, 21, 25, 30–32, 38, 41–48). A few species have small areolas 1 to 2 μm, e.g. *M. microtricha* (Fig. 20), and *M. velutina* (Fig. 24).

2.1.7 Marginal ultimate veins Three types of marginal ultimate veins were observed: (1) fimbriate (Figs. 55, 56, 76), (2) looped (Figs. 49, 50, 57, 60, 69, 72), and (3) incomplete (Figs. 51–54, 58, 61–68, 70, 71, 73–75, 77, 78).

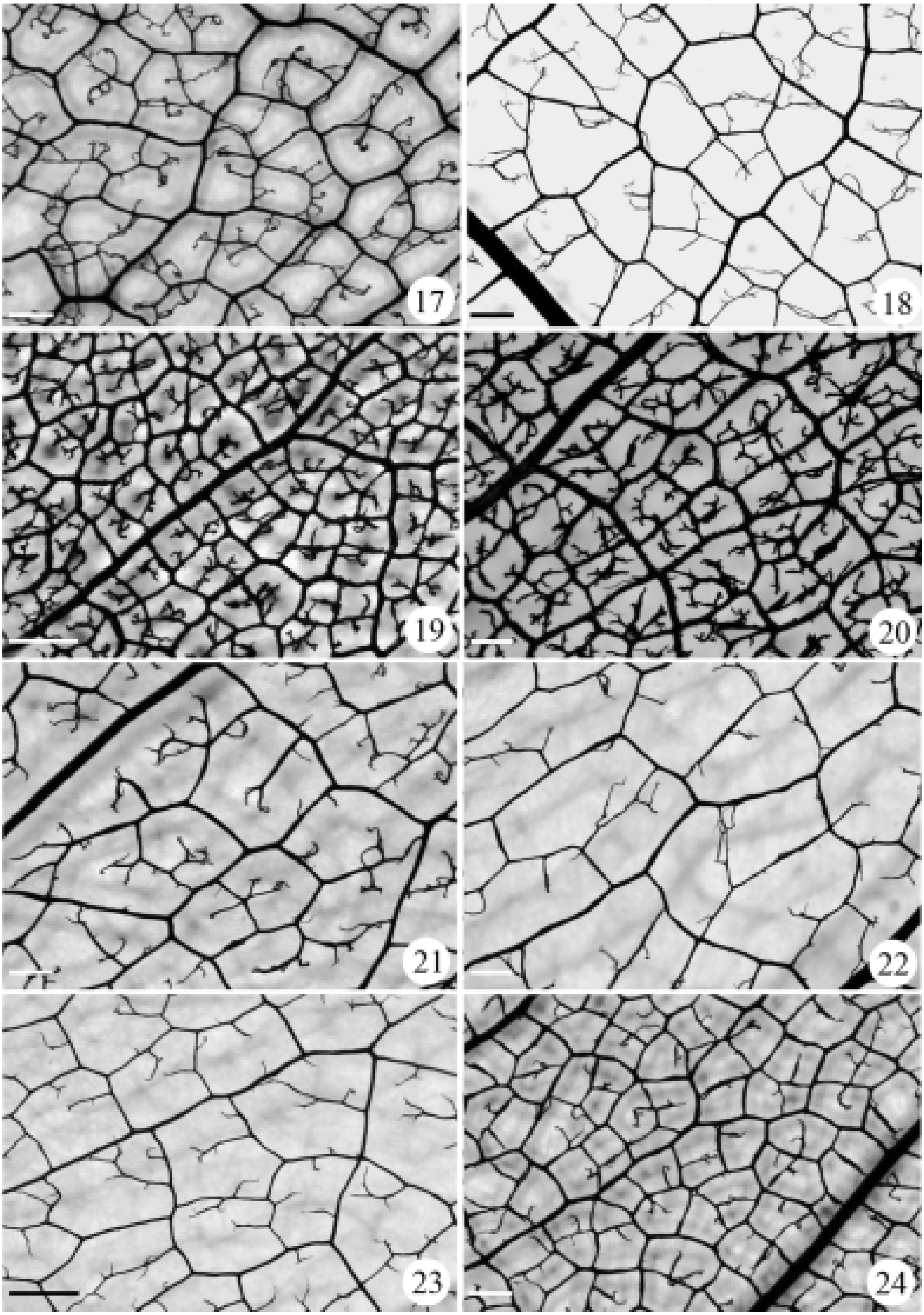
2.2 General description of subtribe Micheliinae

Leaves simple with entire margins, from 4×1.5 cm to 21×7.5 cm. Lamina and its apex highly variable in shape, base usually cuneate or broadly cuneate, obtuse or rounded. Venation camptodromous pinnate. Primary veins moderate to stout, straight, occasionally slightly curved at base. Secondary veins brochidodromous, or proximally brochidodromous to apically eucamptodromous, enclosed by tertiary and quaternary vein arches, alternate or rarely opposite, 7–24 per side, arising at 30º to 85º. Intersecondary veins few, mainly mixed simple and composite. Tertiary veins percurrent to reticulate; quaternary veins arising from tertiary veins at about 90º. Tertiary and quaternary vein areas usually regularly quadrangular in shape. Higher order veins up to 5th order. Areolas well-developed or imperfect, usually quadrangular or irregular in shape. Veinlets absent, simple, branched 1–3 times, or dendroid. Marginal, ultimate veins incomplete, looped, or fimbriate.

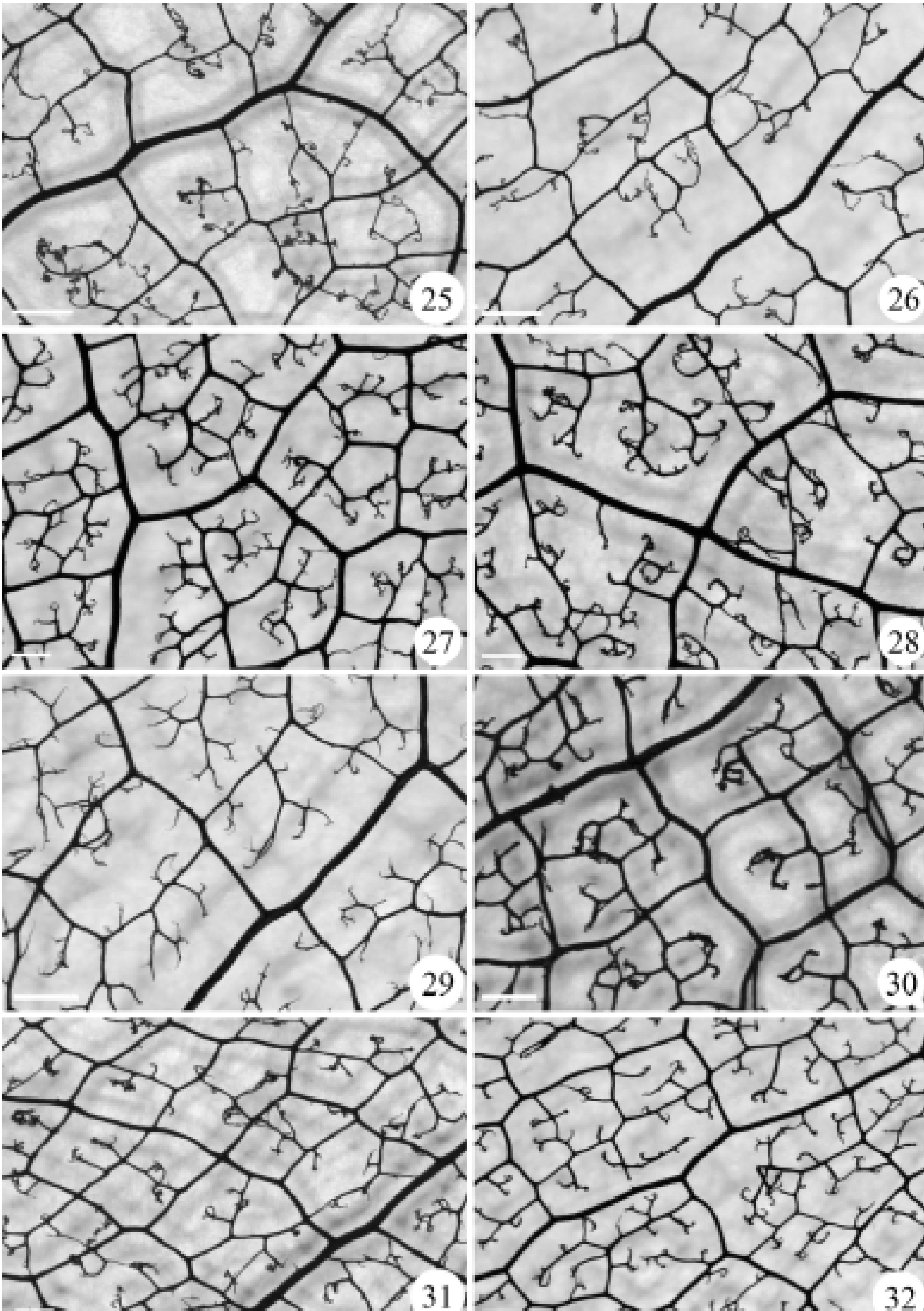
The leaf architectural characters of *Michelia*, *Paramichelia*, and *Tsoongiodendron* are shown in Table 4.

2.3 Phenetic analysis

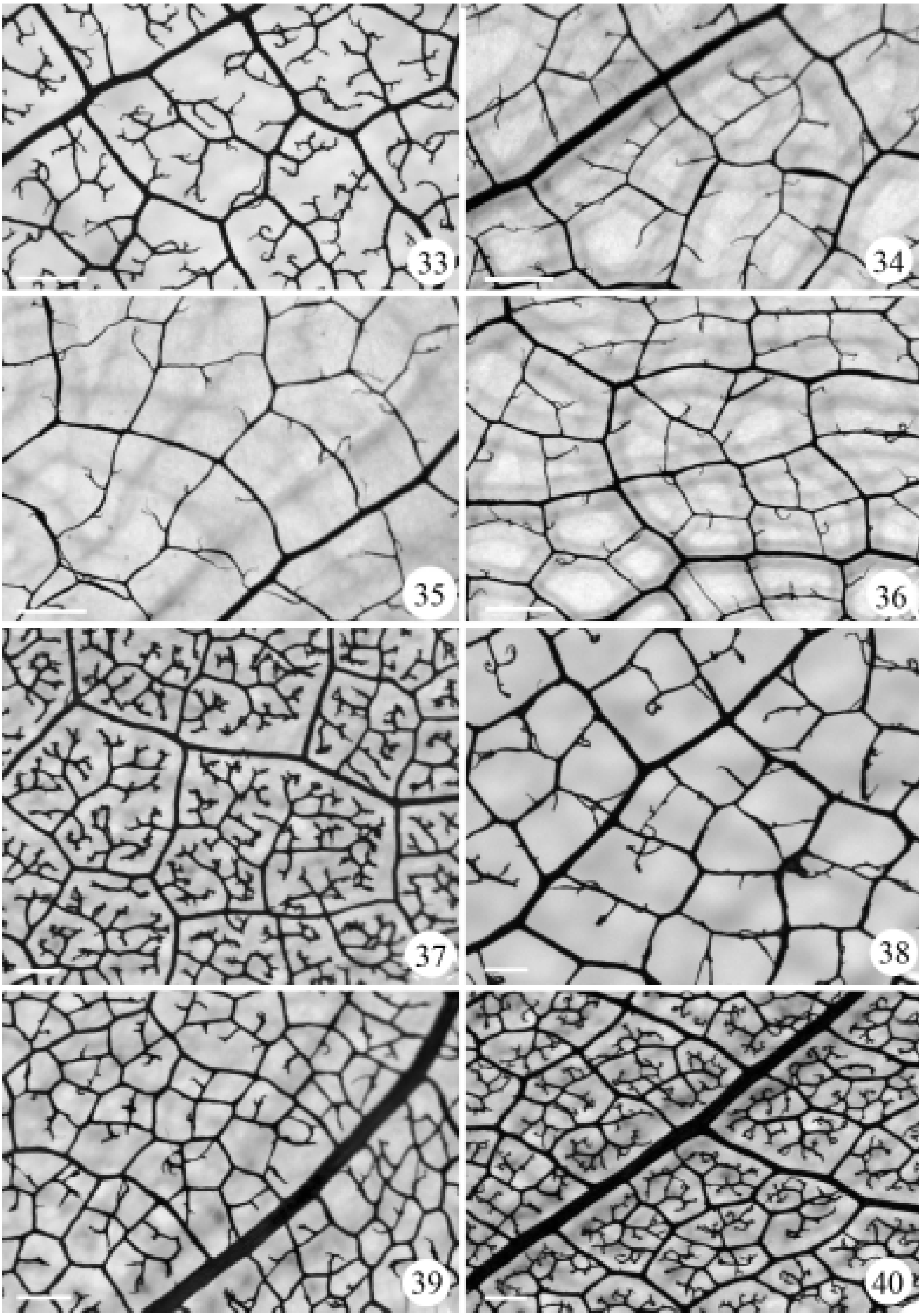
The UPGMA dendrogram (Fig. 79) separated *Liriodendron chinense* from all members of subfamily Magnolioideae. *Michelia*, *Paramichelia* and *Tsoongiodendron* formed a *Michelia* branch and were well separated from *Magnolia*. *Paramichelia baillonii* and *Tsoongiodendron odorum* are nested together and then nested with *Michelia* species. The species of different sections were nested together on separate branches. Section *Michelia* and species (*M. alba, M. champaca, M. doltsopa* et al.) with stipular scars on petioles are nested together, while other species (*M. cavaleriei, M. maudiae, M. macclurei* et al.) without stipular scars on petioles were also grouped together.



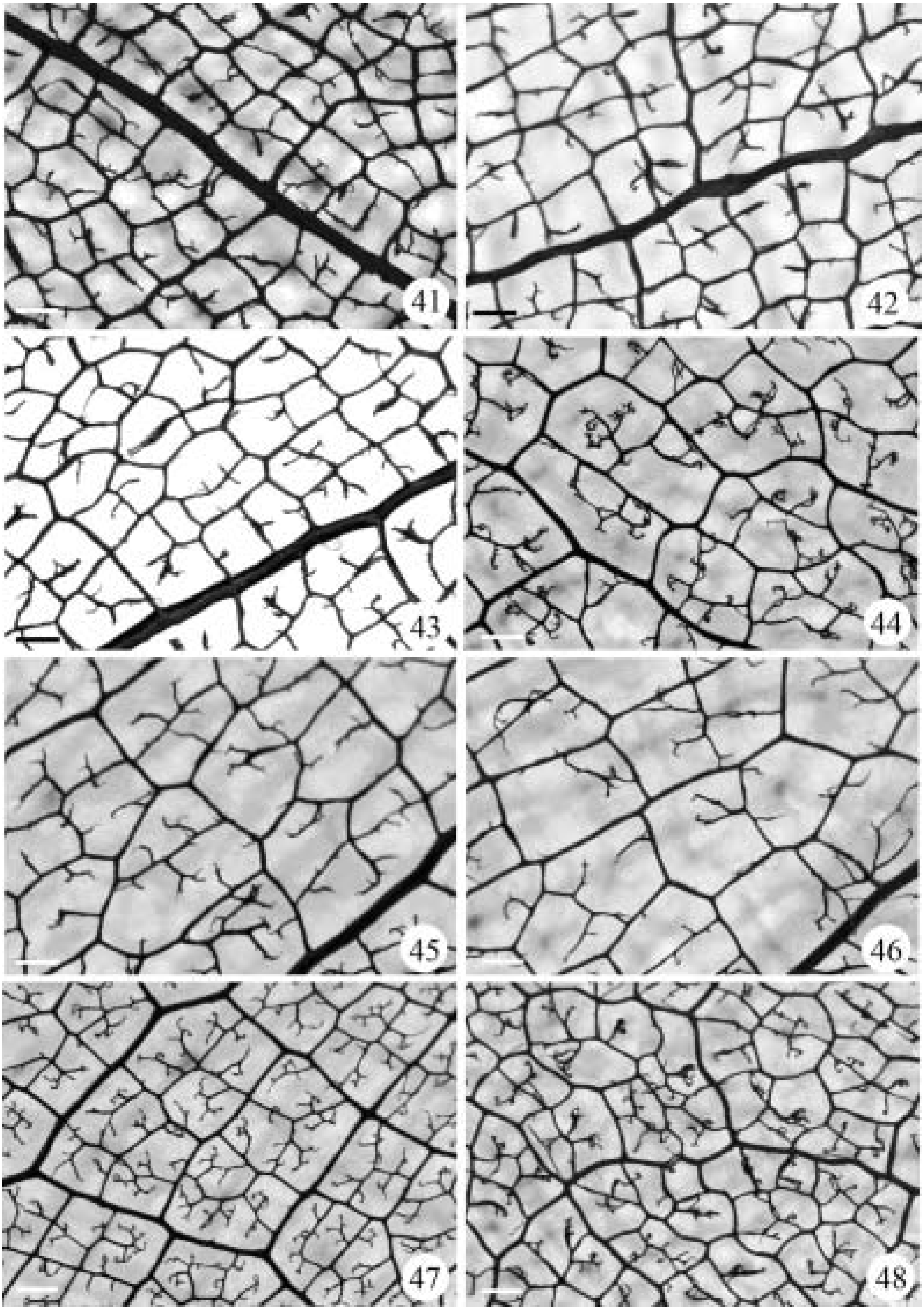
Figs. 17–24. Details of leaf architecture of *Michelia* species. **17.** *M. alba*. **18.** *M. champaca*. **19.** *M. floribunda*. **20.** *M. microtricha*. **21.** *M. wilsonii*. **22, 23.** *M. szechuanica*. **24.** *M. velutina*.
Scale bar: 17, 18, 20, 21, 24=1 μm; 19, 23=1 mm; 22=0.5 mm.



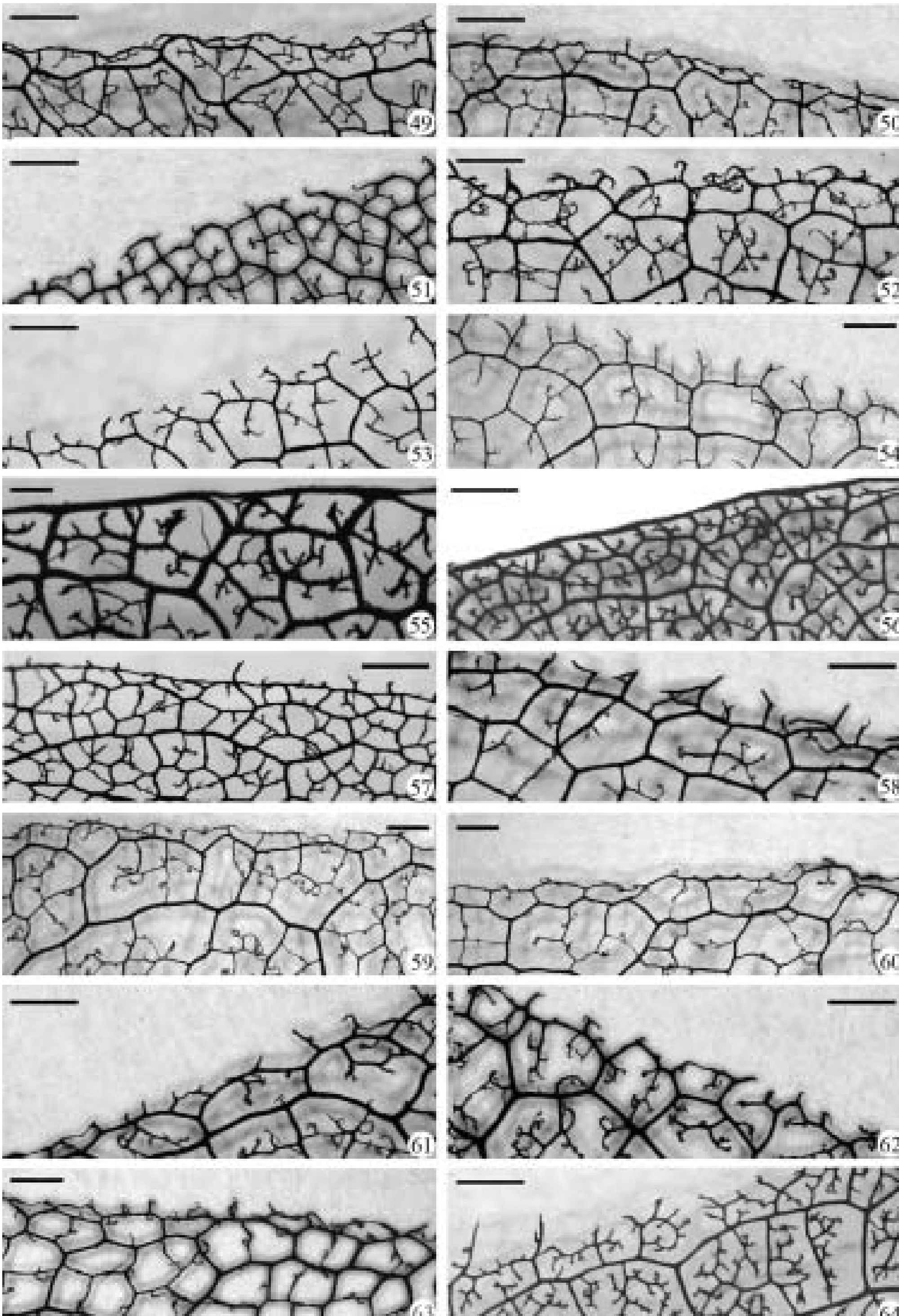
Figs. 25–32. Details of leaf architecture of *Michelia* species. **25, 26.** *M. figo*. **27, 28.** *M. skinneriana*. **29.** *M. crassipes.* **30.** *M. yunnanensis*. **31.** *M. elegans*. **32.** *M. microcarpa*.
Scale bar: 25, 26, 29=1 mm; 27, 28, 31, 32=1 μm; 30=500 μm.



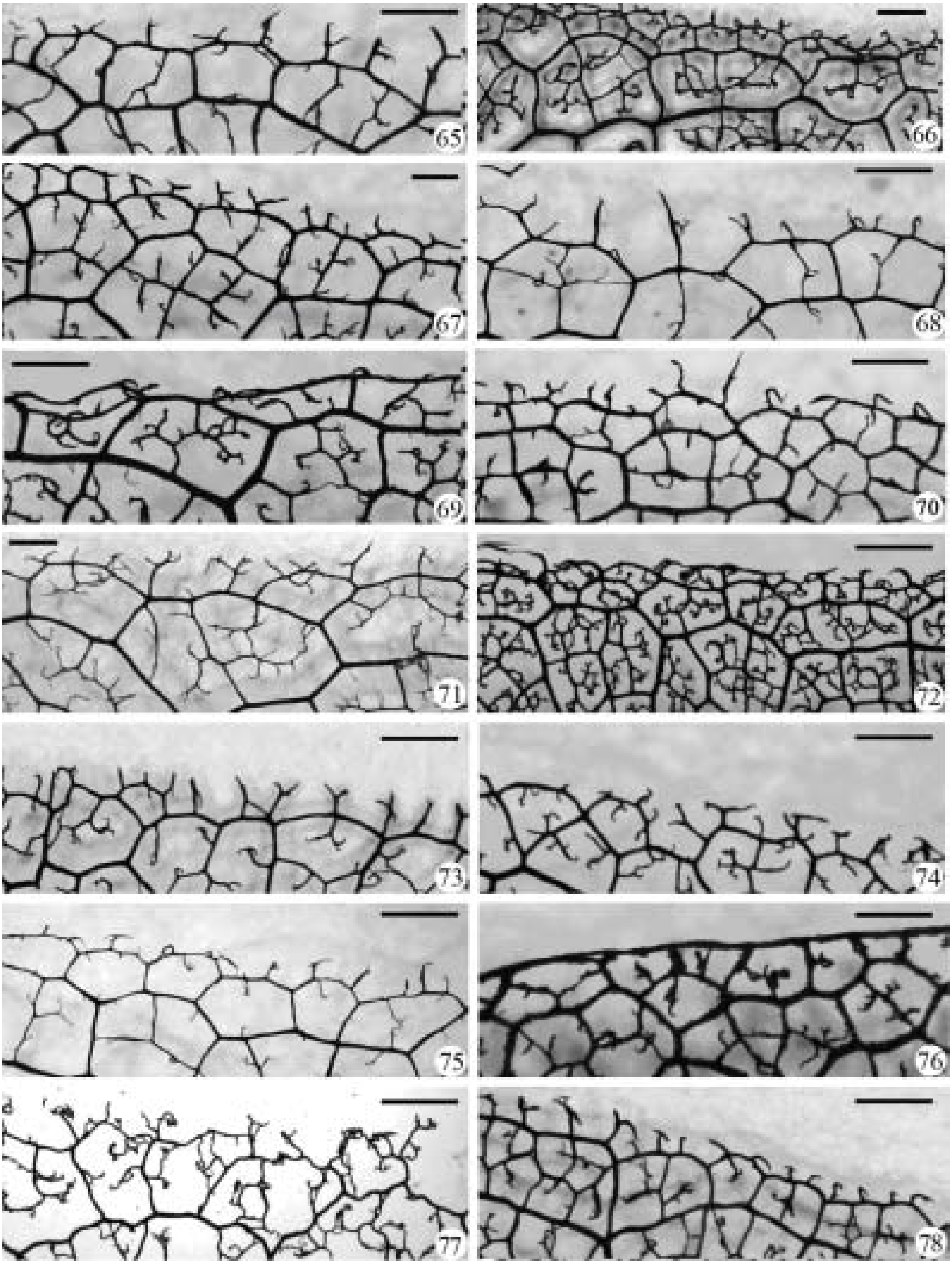
Figs. 33–40. Details of leaf architecture of *Michelia* species. **33.** *M. balansae*. **34.** *M. longistamina*. **35, 36.** *M. platypetala*. **37.** *M. cavaleriei*. **38.** *M. maudiae*. **39.** *M. doltsopa*. **40.** *M. hypolampra*.
Scale bar: 33–36, 39=1 mm; 36, 37, 40=1 μm.



Figs. 41–48. Details of leaf architecture of taxa examined. **41.** *Michelia foveolata*. **42, 43.** *M. foveolata* var. *cinerascens*. **44.** *M. elegans*. **45.** *M. mediocris*. **46.** *M. macclurei*. **47.** *Tsoongiodendron odorum*. **48.** *Paramichelia baillonii*. Scale bar=1 μm.



Figs. 49–64. Marginal ultimate veins in *Michelia*. **49.** *M. alba*. **50.** *M. champaca*. **51.** *M. velutina*. **52.** *M. elegans*. **53.** *M. wilsonii*. **54.** *M. szechuanica*. **55.** M. *microtricha*. **56.** *M. floribunda*. **57.** *M. doltsopa*. **58.** *M. macclurei*. **59, 60.** *M. figo*. **61, 62.** *M*. *skinneriana*. **63.** *M. maudiae*. **64.** *M. cavaleriei*.
Scale bar: 55=500 μm; others=1 mm.



Figs. 65–78. Marginal ultimate veins of taxa examined in subtribe Micheliinae. **65.** *Michelia sphaerantha*. **66.** *M. yunnanensis* **67.** *M. mediocris*. **68, 75.** *M. platypetala*. **69.** *M. balansae*. **70.** *M. foveolata* var. *cinerascens*. **71.** *M. crassipes*. **72.** *M. hypolampra*. **73.** *M. microcarpa*. **74.** *Tsoongiodendron odorum*. **76.** *M. foveolata*. **77.** *M. chapensis*. 7**8.** *Paramichelia baillonii*.
Scale bar=1 mm.

Table 4 Intergeneric comparisons of Magnoliaceae based on leaf architectural characters and morphological characters*

Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Manglietia Bl.	E, D	E	C	U	A, AC	C, D, NC	C	10–16	I	S, D	L, F	4°	P	A	CF	S	T	A	I	S	≥4	E	F
Manglietiastrum Law	E	E	FC	U	BA	C, D	C	13–18	I	S, B	I, L	5°	P	F	EA	S	T	P	I	C	3–5	E	F
Magnolia L.	E, D	E	C	U	AC, E	BC, C	C	10–20	I, W	B	L, F	6°	P	A, F	CF, EA	S, P	T	A	I, L	S	2	E, CO	F
Talauma Juss.	E	E	C	U	A	C	C	14–20	I	S, B	L	4°	P	A	EA	S	T	A	I	S	NF	E	F
Parakmeria Hu & Cheng	E	E	FC	U	A	C	C	10–16	I	S, B	L	4°	P	F	EA	S	T	P	I	C	2	E	F
Kmeria Dandy	E	E	C	U	O, E	BC	C	7–16	I	B	I	5°	P	A	EA	S	T	A	I	C	2	E	F
Alcimandra Dandy	E	E	C	U	A, CA	R, BC	C	12–15	W	S	I	5°	P	F	EA	S	T	P	I	S	2–5	CO	F
Michelia L.	E	E	C	U	A, AC, CA, OA	C, BC, R	C	7–24	I, W	S, B, D	I, L, F	5°	P	A, F	EA	P	A	P	L	S	>2	CO	F
Paramichelia Hu	E	E	C	U	AC	C	C	14–20	W	B	I	5°	P	A	EA	P	A	P	L	C	2–6	E	F
Tsoongiodendron Chun	E	E	C	U	A	C	C	15–20	W	B	I	5°	P	A	EA	P	A	P	L	C	12–16	CO	F
Liriodendron L.	D	P	C	L	T, E	R, CO	MC	6–9	W	B	L	5°	A, P	F	EA	S	T	A	E	S	2	E	A

* 1. Habit: E, evergreen; D, deciduous. 2. Young leaf orientation in vegetative bud: E, erect; P, pendant. 3. Prefoliation: C, conduplicate; FC, flat or curved. 4. Lobation: U, unlobed; L, lobed. 5. Leaf apex: A, acute; AC, acuminate; CA, caudate-acuminate; OA, obtusely acuminate; BA, bluntly acute to rounded; O, obtuse; T, truncate; E, emarginate. 6. Leaf base: C, cuneate; NC, narrowly cuneate; BC, broadly cuneate; D, decurrent; R, rounded; CO, cordate. 7. Venation pattern: C, camptodromous pinnate; MC, mixed-craspedodromous pinnate. 8. Number of secondary veins (paris). 9. Areolas development: I, imperfect; W, well developed. 10. Veinlets: S, simple; B, branched; D, dendroid. 11. Marginal ultimate veins: I, incomplete; L, looped; F, fimbriate. 12. Higher order veins. 13. Stomata type: P, paracytic; A, anomocytic. 14. Stipule attachment: A, stipule adnate to the petiole; F, stipule free from the petiole. 15. Leaf arrangement: EA, evenly arranged at the twigs; CF, crowded into falsewhorls at the ends of the twigs. 16. Branching morphology: S, sylleptic; P, proleptic. 17. Flower position: T, terminal; A, axillary. 18. Gynophore: A, absent; P, present. 19. Anther dehiscence: I, introrse; L, latrorse; E, extrorse. 20. Pre-dehiscence fruiting carpel fusion: S, separate; C, concrescent. 21. Number of ovules in each carpel: NF, numerous or few. 22. Fruit shape: E, ellipsoid, not usually distorted; CO, cylindrical or oblong, usually more or less distorted. 23. Testa and endocarp: F, testa from the endocarp; A, testa adherent to the endocarp. *The classifications of genera follow Law (1996).

3 Discussion

3.1 Leaf architectural characters of subfamily Magnolioideae

Leaf shape of the members of Magnolioideae is highly variable. Leaves of tribe Michelieae are generally smaller in size than those of tribe Magnolieae. The leaf apex is also considerably variable, being acuminate, short-acuminate, acute, short-acute, obtuse or emarginate. Some leaf venation characters of all species examined in subfamily Magnolioideae are similar. Primary veins are all straight or slightly curved. Secondary veins moderate or fine thick, brochidodromous or transforming from brochidodromous to eucamptodromous. Intersecondary veins few or numerous and mainly mixed simple and composite. Tertiary veins in most species surveyed are percurrent to reticulate. Higher orders of veins generally present up to 5th order. But, the others such as areolas, veinlets, marginal ultimate veins provide taxonomic information for specific distinction.

Dendroid veinlets were only observed in *Manglietia* species, *Manglietia glauca* and *Manglietia moto* (Yu & Chen, 1991). They were observed in *Michelia* species, e.g. *M. floribunda* (Fig. 19), *M. microtricha* (Fig. 20), *M. cavaleriei* (Fig. 37), and *M. hypolampra* (Fig. 40) for the first time.

3.2 Systematic implications

3.2.1 Taxonomic value at subfamily level *Liriodendron* comprises two intercontinentally

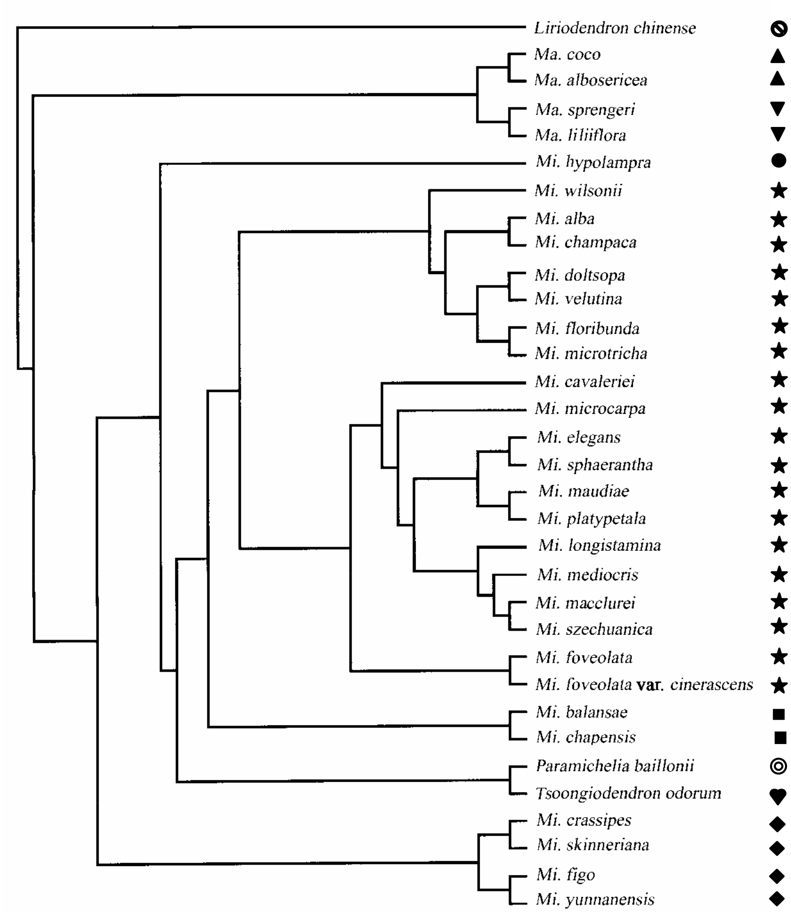


Fig. 79. UPGMA dendrogram of *Michelia* and its related genera based on leaf architectural characters and morphological characters. ⊘, *Liriodendron*; ▲, subgen. *Magnolia*; ▼, subgen. *Yulania*; ★, sect. *Michelia*; ●, sect. *Anisochlamys*; ■, sect. *Dichlamys*; ◆, sect. *Micheliopsis*; ◎, *Paramichelia*; ♥, *Tsoongiodendron*.

disjunct species distributed in E Asia and E North America. It is distinguished from other genera by easily recognizable characters (Table 4), such as extrorsely dehiscent anthers, winged, deciduous and indehiscent samaroid fruits, and testa adherent to the end of the endocarp. Molecular phylogenetic analyses based on chloroplast DNA (cpDNA)(Azuma et al., 2000; Shi et al., 2000; Ueda et al., 2000; Kim et al., 2001, Wang et al., 2003, 2006) and morphological cladistic analysis (Li, 1997b; Xu et al., 2000; Li & Conran, 2003) strongly support the separation of the genus *Liriodendron*. The leaf architectural characters of *Liriodendron* also are distinct from other members of the family. For example, leaves are 2–10 lobed, the apex is truncate or widely emarginate, and there has a mixed-craspedodromous venation pattern. In addition, young leaf orientation in vegetative bud is pendant (Sima et al., 2001) and lower epidermis has anomocytic and paracytic stomates (Lin & Yu, 2004). The phenetic analysis indicated that *Liriodendron* was completely separated from other genera of the Magnoliaceae. Therefore, the division of Magnoliaceae into two subfamilies, Magnolioideae and Liriodendroideae was strongly supported by leaf architectural evidence.

3.2.2 The relationship of *Michelia* and *Magnolia* subgenus *Yulania* The close affinity between *Michelia* and subgenus *Yulania* has been demonstrated by proleptic growth, their cross compatibility, laterally dehiscent anthers, partly undeveloped carpels and cylindrical or oblong, usually more or less distorted fruit (Table 4). In addition, the sequences of several chloroplast DNA regions: *mat*K and *trn*K 3′ intron, *trn*L intron, *trn*T-*trn*L IGS and *trn*L-*trn*F IGS (Ueda et al., 2000), *psb*A-*trn*K and *atp*B-*rbc*L intergenic spacer regions (Azuma et al., 2000) and a morphological cladistic analysis (Li & Conran, 2003) also demonstrated a close relationship between the subgenus *Yulania* and *Michelia*. In the present study, *Magnolia* subgenus *Yulania* is easily distinguished from *Michelia* by leaf shape, leaves crowded into false whorls at the ends of the twigs, deciduous trees or shrubs, as well as gynophore absent, oil cells at the radial verge present and polyploidy (Table 4). In the phenetic analysis subgenus *Yulania* and subgenus *Magnolia* were clustered together and separated from *Michelia* (Fig. 79). The main characters separating subgenus *Yulania* from subgenus *Magnolia* are latrorsely dehiscent anthers and precocious flowers. Subgenus *Magnolia* usually has more primitive characters than those of subgenus *Yulania*, for example, pollen size of subgenus *Magnolia* is larger than that of subgenus *Yulania* (Praglowski, 1974; Xu et al., 2004). The flowers of tribe Michelieae have been perceived to be axillary (Dandy, 1978; Law, 1984, 1996; Liu, 2004). In contrast, they were interpreted as terminal by Nooteboom (1985, 2000), Figlar (2000), Kim et al. (2001), Xu (2003) and Wang et al. (2006). In fact, they are actually produced terminally on axillary short shoots (Fu, 2001) and different from the real terminal flowers of tribe Magnolieae. Therefore it would appear that *Magnolia* subgenus *Yulania* is much closer to *Michelia* than *Magnolia*.

3.2.3 Systematic positions of *Paramichelia* and *Tsoongiodendron* The three genera *Paramichelia*, *Tsoongiodendron*, and *Michelia* are distinguished from each other by fruit. In *Michelia,* the torus elongates after fertilization and the fruiting-carpels are free and longitudinally dehiscent. In *Paramichelia* and *Tsoongiodendron* the carpels are concrescent and form a syncarp, the syncarp of *Paramichelia* being indehiscent or only tardily and irregularly dehiscent, while those of *Tsoongiodendron* are woody and 2-valved dehiscent. The three genera have also been studied thoroughly on pollen morphology (Praglowski, 1974; Xu & Wu, 1995, Xu et al., 1999), leaf epidermis morphology (Baranova, 1972), wood anatomy (Chen, 1958; Zhang, 1974, 1984), karyotype analysis (Chen et al., 1985; Li et al., 1998a, b), chemical constitution (Hao et al., 1999; Hong et al., 1998a, b; Wang et al., 2000; Xiong et al., 2001), morphological cladistic analysis (Li, 1997b; Xu et al., 2000; Li & Conran, 2003), and molecular phylogenetic analysis (Shi et al., 2000; Zeng et al., 2000; Ueda et al., 2000; Kim et al., 2001; Wang et al., 2006). All the results have demonstrated a close relationship among *Michelia, Paramichelia* and *Tsoongiodendron*. Therefore we agree that *Paramichelia* and *Tsoongiodendron* should be reduced to synonyms of *Michelia*.

3.2.4 Infrageneric classification and systematic positions of some species of *Michelia* The phenetic analysis demonstrated that leaf architectural characters and morphological characters can provide useful taxonomic information for infrageneric classification within *Michelia*. The four sections established by Dandy (Praglowski, 1974) were well supported, while two subgenera established by Law (1984) were not supported for the two sections of subgenus *Michelia*, i.e., sect. *Michelia* and sect. *Micheliopsis*, which were widely separated in the dendrogram. Law (1996) put many species that were placed in sect. *Michelia* by Chen & Nooteboom (1993) into sect. *Anisochlamys*, such as *M. foveolata*, *M. cavaleriei* etc., in addition to *M. hedyosperma* (a synonym of *M. hypolampra*). The outer tepals of *M. hypolampra* are membranous and narrow, while those of the other species put in sect. *Anisochlamys* by Law are more or less fleshy and usually similar to the inner tepals. Therefore, Law’s treatment of sect. *Anisochlamys* should not be followed.

In leaf architecture and systematics of the Hamamelidaceae (s.l.), Li and Hickey (1988) thought that the development of marginal ultimate veins progressed from incomplete through looped to fimbriate. In this study, we observed that most species had incomplete or looped marginal ultimate venation, and a few of species possessed fimbriate marginal ultimate venation. On the other hand, we found most species had well developed areolas. General evolutionary trends were represented by increasing regularity in low and high order venation, as suggested by the leaves of fossil angiosperms found so far (Hickey & Wolfe, 1975; Hickey, 1977; Hickey & Doyle, 1977; Doyle, 1978). Using the criterion of increase in regularity, we suggest the possible evolutionary trend for leaf architectural characters of *Michelia* is as follows: (1) areolas imperfect→well developed; (2) veinlets dendroid→veinlets branched→ veinlets simple or absent; (3) marginal ultimate veins incomplete→looped→fimbriate.

Like other morphological or palynological characters, leaf architectural characters can be a source of information for the systematic position of species. In the present study, two or three samples of the same species were examined. The results show that leaf architectural characters are relatively constant within one species, e.g. *M. figo* (Figs. 25, 26, 59, 60), *M. skinneriana* (Figs. 5, 6, 27, 28, 61, 62), *M. platypetala* (Figs. 35, 36, 68, 75), and *M. elegans* (Figs. 31, 44). In particular, areolas, veinlets, and marginal ultimate veins do provide valuable information for clarifying the interspecific relationships within *Michelia*. A key for the identification of taxa examined is presented.

3.2.4.1 *M. floribunda* and *M. microtricha* *M. microtricha* was recognized by Chen & Nooteboom (1993), distinguished from *M. floribunda* by indumentum with minute hairs and longer brachyblasts. Li (1997a) reduced it to a synonym of *M. floribunda* on account of leaf shape, indumentum and length of brachyblast being continuously variable, and unstable characters. No significant differences in leaf architectural characters were found between them in this study (Table 5) and they were nested together in the phenetic UPGMA analysis (Fig. 79). Therefore it would seem reasonable to treat *M. microtricha* as conspecific with *M. floribunda* .

3.2.4.2 *M. chapensis* and *M. microcarpa* *M. chapensis* was described by Dandy in 1929 from material collected in Chapa, Vietnam. It is a widespread species in China. *M. microcarpa* was described by Chen & Yang (1988) from material collected in Maguan, Yunnan in China. Chen & Nooteboom (1993) reduced the latter to a synonym of *M. chapensis*. However, on the basis of its glabrous gynoecia and leaves with dense and conspicuously elevated reticulate veins on both surfaces when dry, Sima (2001) concluded that *M. microcarpa* could be easily distinguished from *M. chapensis*. Leaf architectural characters were found to differ substantially in this study (Table 5; Figs. 32, 73, 77), supporting the conclusion that *M. chapensis* and *M. microcarpa* are completely different. Therefore it appears more reasonable to recognize *M. microcarpa* as a distinct species than to treat it as a synonym of *M. chapensis*.

3.2.4.3 *M. platypetala, M. cavaleriei,* and *M. maudiae* Chen & Nooteboom (1993) reduced *M. platypetala* to a synonym of *M. cavaleriei*. Law (1996) treated all three as distinct species in Flora Reipublicae Popularis Sinicae. Sima (2001) lowered *M. platypetala* to a variety of *M. maudiae*. Our observations of leaf architectural characters and morphological characters suggest that the three species are substantially different (Figs. 35, 37, 38, 63, 64, 75; Table 5). *M. platypetala* should be recognized as an independent species.

3.2.4.4 *M. szechuanica* and *M. wilsonii* *M. szechuanica* was described by Dandy (1928) from a collection by Wilson from Kai Xian, Sichuan. It was widely recognized in China (Law, 1983, 1996; Figlar, 2000), but was reduced to a synonym of *M. wilsonii* by Chen and Nooteboom (1993), and Li (1997a) and Sima (2001) treated it as a subspecies of *M. wilsonii*.

Table 5 Differences of leaf architectural characters, morphological characters and geographical distributions of some taxa in *Michelia**

Taxon	Morphological characters	Leaf architectural characters								Distribution
		Lamina				Areolas		Veinlets	MUV	
		Shape	Size (cm)	Apex	Base	Size	NV			
M. maudiae	buds, young twigs, stipules outside, leaves beneath, petiole, brachyblasts, bracts outside, and gynoecium pale green to glaucous when dry; tepals 9	E	7-15× 3.5-6	OS	O	2-3 μm	1	S	L	S Zhejiang, Fujian, Hunan, Jiangxi, Guangdong, Hongkong, Guangxi and Guizhou
M. platypetala	buds, young twigs, and young leaves rufous sericeous; tepals 9	E	17-23× 6-11	OS	C	1-2 mm	1	S,	I	W Hubei, SW Hunan, E Guangdong, NE Guangxi, and E Guizhou
M. cavaleriei	buds, young twigs, stipules, petioles, brachyblasts, and bracts outside densely appressed-pubescent with fine, short to long, straight, clear to brown, glossy hairs；tepals 12	E	20-22× 8-11	AC	C	1-2 mm	3–4	D	I	SE Sichuan, NE & S Guizhou, NW Guangxi, and SE Yunnan
M. chapensis	appressed puberulent gynoecia and leaves with sparse and inconspicuous reticulate veins when dry	NO	6.5–15× 3.5–6	A	C	1–1. 5 mm	2–3	TB	I	S Jiangxi, W Hunan, N Guangdong, NE & SE Guangxi and Vietnam
M. microcarpa	glabrous gynoecia and dense and conspicuous elevated reticulate veins on both surfaces of leaves when dry	E	6–8.5× 3.5–5	A	C	0.1– 0.25 mm	2–3	OB	I	Maguan,Yunnan
M. floribunda	the indument with minute hairs and the longer brachyblasts	NE	7–14× 2–4	AC	C	2–4 μm	1	D	F	Yunnan, Sichuan, W Hubei, and Myanmar
M. microtricha	Appressed-tomentellous with minute, straight, brown to gray hairs, glabrescent and the short brachyblasts	E	6.5–12× 3–4.5	A	C	1–2 μm	1	D	F	Yunnan
M. wilsonii	possessing spreading hairs; stipular scars 2–4 mm long	NE	10–15× 3.5–7	A	C	3–6 μm	1	OB	I	C & W Sichuan
M. szechuanica	possessing appressed hairs without stipular scars	NE	9–15× 3–6	SC	C	1–2 mm	1	S	I	W Hubei, S & SE Sichuan, N Guizhou and NE Yunnan

*Shape: E, elliptic; NE, narrowly elliptic; NO, narrowly obovoid. Apex: A, acute; AC, acuminate; OS, obtusely short-acute; SC, sharply caudate-acuminate. Base: C, cuneate; O, obtuse. Veinlets: S, simple; OB, 1–2 times branched; TB, 2–3 times branched; D, dendroid. MUV: Marginal ultimate veins; I, incomplete; L, looped; F, fimbriate. NV: Number of veinlets per areola.

The main morphological difference between them is that *M. szechuanica* does not have stipule scars on its petioles, while *M. wilsonii* does. Leaf architectural characters were also different in the branching of veinlets (Figs. 21–23) and presence of prominent arches on adaxial surfaces of leaves, and they are also well separated in the dendrogram (Fig. 79). This

would suggest that *M. szechuanica* should be recognized as a distinct species rather than a subspecies of *M. wilsonii*.

4 Conclusions

Leaf architectural characters provide useful taxonomic information in *Michelia*. The four sections of *Michelia* established by Dandy (Praglowski, 1974), i.e., sect. *Michelia*, *Micheliopsis*, *Dichlamys* and *Anisochlamys*, are well supported by the phenetic analysis of leaf architecture combined with other morphological characters, but the two subgeneric subdivision of *Michelia* established by Law (1996) seem to be unacceptable. *Paramichelia* and *Tsoongiodendron* are not separable from *Michelia* in characters of leaf architecture and floral morphology except in their concrescent fruits, and on this basis it seems more reasonable to reduce them to synonyms of *Michelia*.

Key to the *Michelia* taxa examined with reference to the leaf architectural characters

1. Stipular scars on petioles present.
  2. Petioles less than 5 mm.
    3. Areolation well developed.
      4. Lamina elliptic or narrowly elliptic……………………1. **M. figo**
      4. Lamina obovate or narrowly obovate……………………2. **M. yunnanensis**
    3. Areolation imperfect.
      5. Veinlets 2–4 times branched……………………3. **M. skinneriana**
      5. Veinlets 2–3 times branched, rarely one time branched……………………4. **M. crassipes**
  2. Petioles longer than 5 mm.
    6. Marginal veins fimbriate.
      7. Areolas median, 1 μm<Areola size (As)≤2 μm……………………5. **M. floribunda**
      7. Areolas small, 2 μm<As≤1 mm……………………6. **M. microtricha**
    6. Marginal veins looped or incomplete.
      8. Marginal veins looped.
        9. Areolas small, 1 μm<As≤2 μm…………………… 7. **M. doltsopa**
        9. Areolas median, 2 μm<As≤1 mm.
          10. Stipular scars nearly to half of petiole length……………………8. **M. alba**
          10. Stipular scars longer than half of petiole length……………………9. **M. champaca**
      8. Marginal veins incomplete.
        11. Veinlets simple.
          12. Areolas small, 1 μm<As≤2 μm……………………10. **M. velutina**
          12. Areolas median, 2 μm<As≤1 mm……………………11. **M. wilsonii**
        11. Veinlets 1–2 times branched.
          13. Quintenary veins reticulate……………………12. **Paramichelia baillonii**
          13. Quintenary veins alternate and opposite percurrent……………………13. **Tsoongiodendron odorum**
1. Stipular scars on petioles absent.
  14. Veinlets dendroid.
    15. Marginal veins looped……………………14. **M. hypolampra**
    15. Marginal veins incomplete……………………15. **M. cavaleriei**
  14. Veinlets simple or 1–3 times branched.
    16. Areolation imperfect.
      17. Marginal veins looped……………………16. **M. balansae**
      17. Marginal veins incomplete……………………17. **M. chapensis**
    16. Areolation well developed.
      18. Quaternary veins alternate and opposite percurrent.
        19. Marginal veins fimbriate…………………… 18. **M. foveolata**
        19. Marginal veins incomplete……………………19. **M. foveolata** var. **cinerascens**
      18. Quaternary veins reticulate.
        20. Veinlets 2–3 in each areola……………………20. **M. microcarpa**

20. Veinlets one, rarely 2 in each areola.
 21. Areolas quadrangular.
  22. Veinlets one time branched……………..………………..……..….…21. **M. elegans**
  22. Veinlets simple.
   23. Areolas median, 2 μm<As≤1 mm.………………….….….….…22. **M. maudiae**
   23. Areolas large, >1 mm………………………..……...……..23. **M. platypetala**
 21. Areolas polygonal.
  24. Mesophyll; lamina obovate-oblong or oblong.........................…24. **M. sphaerantha**
  24. Notophyll; lamina elliptic or obovate.
   25. Areolas median, 2 μm<As≤1 mm.
    26. Lamina obovate or elliptic-obovate…………..…….………25. **M. macclurei**
    26. Lamina rhombic-elliptic..…………………...………..….26. **M. mediocris**
   25. Areolas large, >1 mm.
    27. Lamina appressed indumentum on both surfaces…..…....27. **M. szechuanica**
    27. Lamina glabrous……………………….....…………....28. **M. longistamina**

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国产木兰科含笑亚族植物的叶结构及其分类学意义

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摘要 为了探讨含笑亚族Micheliinae植物属间关系以及含笑属*Michelia*属下等级的划分和一些种的分类学地位, 利用放大镜和体视镜对国产含笑亚族植物3属共28个分类群的叶结构特征进行了观察与研究。结果表明: 含笑属、合果木属*Paramichelia*和观光木属*Tsoongiodendron*植物的脉序类型、一级脉、二级脉及其间脉和三级脉等特征表现出较高的一致性, 三属间无明显的划分界限; 但是, 盲脉及其分支、网眼的发育和大小、叶缘末级脉等叶结构特征存在种间差异。在含笑属中, 树状盲脉首次被观察到。用UPGMA对所研究28个分类群、木兰属*Magnolia*两个亚属各2种和鹅掌楸*Liriodendron chinense*的叶结构特征和形态学特征共46个性状进行聚类分析。分析结果表明: (1)合果木*P. baillonii*和观光木*T. odorum*与含笑属的种聚为一支, 因此, 支持将合果木属和观光木属归并入含笑属; (2)这些特征为含笑属内组的划分提供了分类学意义; (3)基于叶结构特征、形态学特征、地理分布、聚类分析, 对含笑属内一些种类的分类地位进行了讨论。

关键词 木兰科; 含笑属; 合果木属; 观光木属; 盲脉; 分类学意义